

## SOME ASPECTS OF THE REPRODUCTIVE BEHAVIOR OF *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE)

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### ABSTRACT

The duration of the reproductive and courtship periods, the number of individual matings, and the number of egg sacs and their viability were measured in *Lycosa tarentula fasciiventris* under laboratory conditions. We found that the reproductive period is very short, lasting for a month from July to August. Both the males and the females can mate more than once. Female receptivity is related to age and reproductive state: receptivity is less in both old and previously mated females. Neither the size nor the viability of cocoons is related to the number of female matings. Our results are interpreted in relation to optimization of egg fertilization.

### RESUMEN

En *Lycosa tarentula fasciiventris*, hemos medido la duración del periodo reproductivo y del cortejo, el número de apareamientos de cada individuo, el número de puestas de cada hembra y su viabilidad en el laboratorio. Hemos encontrado que el periodo reproductivo es muy breve, de alrededor de un mes, comprendido entre julio y agosto. Tanto los machos como las hembras se aparean más de una vez, estando relacionada la receptividad de la hembra con su edad y con su estado reproductivo: tanto las hembras "viejas" como las previamente apareadas muestran una receptividad menor. Ni el tamaño ni la viabilidad de la puesta están relacionados con el número de apareamientos realizados por la hembra. Nuestros resultados se interpretan en relación a la optimización de la fertilización de los huevos.

### INTRODUCTION

Theoretical models which try to explain the reproductive tactics of males and females have been developed which usually refer to species in which both the number of eggs produced by females and the investment of the male in the offspring are very low (Gould 1982; Huntingford & Turner 1987). It has been predicted that females will try to invest in only a few matings, will take less advantage of multiple mating, and will choose the male with which to mate (Halliday 1983, 1986; Huntingford & Turner 1987), whereas males will compete for females.

*Lycosa tarentula fasciiventris* Dufour is a burrowing spider from the Iberian peninsula. In central Spain, populations are distributed in open and arid areas (Barrientos 1978) with poor plant cover. Temperature conditions are greatly

variable, both seasonally and daily. Animals live in burrows throughout all their developmental stages, except the adult males, with adult females showing the greatest location stability (pers. obs.). Individual development takes place over a period of about 22 months, and animals reach their adult instar at about the end of spring in their second year of life. Reproduction takes place shortly after, at the beginning of the summer (pers. obs.). During this time, males are found wandering in search of females in areas in which isolated individuals are very distant from one another. Male survival after the reproductive period is nil, whereas females may survive for several months. Under laboratory conditions, males may live as long as 2 or 3 months after summer, while females may live as much as 1.5 to 2 years. Like many other spider species (Fink 1986), females show a kind of behavior towards their egg sac that has been called "maternal" (Horel & Krafft 1986). They carry with them both their egg sac and their spiderlings, thus leading to changes in female responsiveness (pers. obs.).

The interindividual distances will make the chance of finding a mate low for both the males and females. Under these conditions, males might be expected to compete for females. However, laboratory observations have shown male agonistic interactions being settled in a ritualized way and leading to apparently paradoxical results (smaller or intruder male wins). Given the fact that female longevity is higher, postcopulatory guarding behavior is not to be predicted (Austad 1984). Competition between females might also be expected (Fernández-Montraveta & Ortega, in press), as well as female choice, given that female investment is greater than in the male.

In this paper we try to measure some reproductive behavior variables in order to evaluate how they fit the expected patterns according to whether or not animals are behaving in ways that lead to relatively high reproductive payoffs.

## MATERIAL AND METHODS

In this study, 71 adult males and 66 adult females were used. All the animals were from the countryside around the "Universidad Autónoma de Madrid". All the males and 56 females were collected during the spring of 1985 and 1986, when immature, usually at their penultimate developmental stage. The remaining females (10) were collected as adults around the end of winter, 1985. Animals were kept isolated under controlled conditions of temperature ( $25 \pm 5^\circ\text{C}$ ), 10:14 light:dark cycle, and fed twice weekly with a blowfly outside the observation periods.

Animals were observed in their adult stage. The observation chamber was a terrarium occupied both by the male and the female for a week before the observation took place. Previous to the observation, animals were visually isolated from one another; the partition was removed to carry out the observation. We used only males having molted to adults during the year of the study, 37 females having also molted during this year ("young females") and 29 adult females 1 year old when the observation took place ("old females"). This last group comprised both the animals collected when adults, presumably "copulated females", and animals collected when immature that have not copulated during their first adult year ("virgin females"). The decision to consider the first group of females as copulated ones was made *a posteriori*: all of these animals later constructed a viable egg sac, without copulating, in the laboratory.

During July and August of both 1985 and 1986, we observed 254 pairs of animals. Pairs were formed at random with regard to individual variables. Every animal was observed at first through the first week after molting, and at least twice on different days. If copulation occurred, the second observation was made during the first week after copulation and so on. Each observation lasted at least 30 min. Females were usually inside their burrow, so interaction took place there. We have considered that interaction began when the male was 2 or 3 cm away from the female burrow, and oriented towards it. When an interaction took place, the observation was prolonged as long as it lasted. Interaction finished when the male moved away from the female nest and ceased orientation. Ninety-five interaction sequences were obtained and analyzed. After the observation period, animals were kept in the laboratory and observations about the subsequent reproductive activity were made.

We measured (i) the date on which molting to adulthood took place, (ii) the date of copulation, (iii) the result (copulation/retreating before copulation) of interactions, (iv) the number of matings for both sexes, (v) the courtship and copulation durations, (vi) the number of egg sacs for every female, (vii) the weight of each egg sac and (viii) the number of spiderlings emerging from each egg sac. Results have been compared with regard to four female groups, two related to female age (young females/old females) and the other related to their previous reproductive history (virgin female/copulated female).

As for quantitative variables, their mean values and standard deviations have been calculated. In order to compare the means, a variance homogeneity test was made before applying the *t*-test.

In order to measure how the quantitative variables are related, the correlation coefficient was calculated and the Chi-square test was applied to measure the independence of the results with regard to the different female groups.

## RESULTS

In 1986, both male and female molting in the laboratory reached a peak about the second week of June. In 1985, the same peak was observed about the third week of June in males and the second week of July in females. Copulation was observed from the middle of June to the first week of August, and the copulation rate increased steadily with time. Peaks were observed at the end of July (1986) and the beginning of August (1985).

Forty-six copulations were observed in all. When in the second year of their adult life, only 42% of the females were receptive if virgin, as contrasted to 81% of the young virgin females. The old, previously mated females were not receptive at all (Table 1). We tested the dependence between receptivity and "age" and "previous reproductive history" separately. Female receptivity significantly depends on the female's previous reproductive history ( $\chi^2 = 5.53$ ,  $p < 0.05$ ); virgin females were receptive in 68% of the cases in contrast to 39% of the previously copulated females. It also depends significantly on age ( $\chi^2 = 19.80$ ,  $p < 0.05$ ); 78% of the females were receptive when young and only 28% when old.

Forty-eight per cent of the males observed succeeded in copulating, in contrast to 68% of the females. Both the males and the females can mate more than once under laboratory conditions (Table 2). Sixty-five percent of the males copulated

Table 1.—Female receptive response to mating with regard to its age and its previous reproductive history (PRH).

| PRH       | Variable | Receptive Response |    |       |
|-----------|----------|--------------------|----|-------|
|           |          | Yes                | No | Total |
| Virgin    | young    | 30                 | 7  | 37    |
|           | old      | 8                  | 11 | 19    |
| Copulated | young    | 8                  | 5  | 13    |
|           | old      | 0                  | 10 | 10    |
| Total     |          | 46                 | 33 | 79    |

once and 35% twice, but no male copulated more than twice. Among the females, 82% were receptive only once, 16% twice and 3% more than twice.

Mean courtship duration was  $23.4 \pm 21.25$  min. The mean duration when the courted female was virgin, regardless of age, was  $17.6 \pm 17.34$  min. The mean courtship duration when females were young virgins was  $20.1 \pm 20.35$  min, and  $15.3 \pm 13.70$  min when old virgins ( $t = 0.42$ , ns). The mean courtship duration when the female was young and had previously copulated was  $25.0 \pm 16.26$  min and  $40.7 \pm 28.77$  min when the courted females were old, previously copulated ones. There is a statistically significant difference between the mean courtship duration of the virgin group, regardless of age, and the old, previously copulated group ( $t = 2.14$ ,  $p < 0.05$ ). The observed mean copulation duration was  $89.2 \pm 31.1$  min.

Data from 35 first egg sacs were analyzed. Of these, 30 were from females having copulated once and five from females having copulated twice or more. Mean weight of the egg sacs was  $0.30 \pm 0.10$  g in the first group and  $0.22 \pm 0.06$  g in the second ( $t = 1.60$ , ns). We observed no greater size in the egg sacs of females that copulated more than once. Spiderlings emerged from 21 egg sacs in the first case and three in the second. Mean number of emerged spiderlings was  $117.2 \pm 51.8$  in the first group, and  $105.67 \pm 31.41$  in the second. The correlation coefficient between egg sac weight and number of living spiderlings was 0.61 ( $p < 0.05$ ).

There were 20 second egg sacs, both by females collected as adults and by females kept in the laboratory for more than 1 year. The second egg sac was then produced in the second year the females lived, not being preceded by mating during that year. Living spiderlings emerged from 10 of them (50%).

## DISCUSSION

We measured some synchronization between the molting dates of males and females, providing mating is concentrated during a very short period of time. We

Table 2.—Number of males and females copulating once, twice, or more than twice.

| Sex    | Number of matings |    |    | Total |
|--------|-------------------|----|----|-------|
|        | 1                 | 2  | >2 |       |
| Male   | 22                | 12 | 0  | 34    |
| Female | 31                | 6  | 1  | 38    |
| Total  | 53                | 18 | 1  | 72    |

consider that the difference observed between the two years might indicate that the individual molting date is adjusted to the changing environmental factors. Since animals for the most part were captured shortly before their molt to adults, we think these factors could have affected individual molting dates.

The nature of the factors determining female receptivity, related to its age and previous reproductive history, might explain the observed shortness of the period in which mating took place. This time limitation suggests that competition between males is reflected in their early maturation rather than by direct aggression, accounting for the earlier maturation peak shown by males, especially in our first year of study. This hypothesis might also explain the apparently paradoxical resolution of male interactions we observed in this species.

Both the males and the females we observed can achieve more than one mating, as do many other spider species (Jackson 1979; Austad 1984; Christenson 1984; Breene & Sweet 1985; Brown 1985). Our results do not suggest multiple mating to be related to greater success of the first female egg sac in this species. Since sexual partners seem to be limited, the multiple-mating benefit for females might be related to the sperm supply (Austad 1984; Christenson 1984), given the egg sac size and the need for sperm to be stored in order to be successively used (Christenson et al. 1985). The greater cost of rejecting a persistent male rather than accepting copulation as the reason for this multiple mating (Austad 1984; Christenson et al. 1985) does not seem to be the most appropriate explanation because non-receptive females of this species are rather aggressive (Ortega et al. 1986), like other lycosid females (Rovner 1972). The need for a sperm supply, along with the possible benefit of genetic diversity among offspring (Christenson 1984; Huntingford 1984; Huntingford & Turner 1987) could be the reason why female reproductive strategy consists of accepting matings with several males during one reproductive period.

Female sperm storage, as well as multiple egg sacs seems to be a general pattern in spiders (Austad 1984; Christenson 1984; Blandin & Célérier 1986; Fink 1986). Mating also takes place before the first oviposition in other spider species (Austad 1984; Sadana pers. com.). The advantages of this species concentration of mating in only one reproductive period should be explored. We think this concentration might be a consequence of the great seasonal climatic differences, given the lesser inter-egg sac period shown by other lycosid spiders.

Since, in the species we have studied, female investment is greater than the male's, female choice should be expected (Huntingford 1984). With regard to the kind of individuals with which a female mates, its behavior when virgin does not seem to be discriminative (Ortega et al. 1986). Female choice has been postulated in a few cases (Austad & Thornhill 1986), as taking place when females have already copulated (Jackson 1982). This is interpreted as first mating guaranteeing egg fertilization, offspring quality being increased in the following matings (Halliday 1983). The occurrence of multiple mating with lesser receptivity of previously mated females agrees with that prediction.

The duration of male courtship with regard to female reproductive status might indicate male behavior is based on investing a fair amount of time courting every female found, even if she does not show any receptive response at first (Ortega et al. 1986).

To reach the adult stage early and to succeed in mating with all the females he finds would define the male reproductive tactic. Females, on the other hand, will

try to choose the male to mate with after the sperm supply has been guaranteed, and to reduce the copulation duration to the effective insemination period. Conflict of interests will arise over these factors. Males are expected to prolong the copulation duration beyond the effectiveness of insemination, whereas females are expected to try to reduce the total copulation duration to just the effective insemination periods. More data on copulation in this species is needed to test this hypothesis.

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